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## Downed Wood Microclimates and Their Potential Impact on Plethodontid Salamander Habitat in the Oregon Coast Range

### Abstract

Downed wood provides important faunal microhabitat in forests for numerous invertebrate taxa, small mammals and amphibians. Habitat suitability of downed wood as refugia is an increasing concern in managed Pacific Northwest forests, where overstory reduction may result in both reduced downed wood recruitment and increased temperatures within logs. We examined temperature profiles in western Oregon to assess differences in thermal regimes of logs and soil relative to summer air temperature extremes and their implications with respect to habitat suitability for plethodontid salamanders. Temperature profiles of small- (0.3-0.45 m) and large- (0.7-1.0 m) diameter logs, as well as ambient soil and air temperatures, were measured in a 60-year-old forest stand at two different positions (0-5 m and 35-40 m from stream edge) in three case studies: 1) along a headwater stream with a narrow riparian buffer (~6 m) and moderate upslope thinning; 2) along a headwater stream with a wider riparian buffer (~15 m) and moderate upslope thinning; and 3) along a headwater stream with an unthinned upslope. Streamside and upslope maximum air temperatures measured during July 2006 along all three streams were near or exceeded 30°C, the critical thermal tolerance threshold for western plethodontid salamanders. Streamside and upslope temperatures inside small logs, large logs and soils stayed below critical temperatures. Our results suggest that logs of a wide size range, as well as soils, may provide sufficient protection against thermal extremes in uncut forests and thinned stands with limited overstory.

### Introduction

Microclimate regimes are an emerging concern in managed forest landscapes as it has become apparent that many organisms are dependent on late-successional and old-growth forest conditions (Franklin and Forman 1987, Lehmkuhl and Ruggiero 1991). In particular, some amphibian species are dependent on cool, moist conditions often found in older forests west of the Cascade Range in the Pacific Northwest (Welsh 1990). Impacts of forest management practices on microclimate regimes have been widely studied, ranging from thinning and riparian buffers (Anderson et al. 2007), clearcut and riparian buffers (Brosofske et al. 1997, Rykken et al. 2007) and structural retention (Heithecker and Halpern 2006). However, information about microclimates of specific microhabitat refugia is largely lacking.

Over the past three decades, the importance of downed wood for many fish and wildlife species (Maser et al. 1979, Maser and Trappe 1984, Brown 2002), and also its importance for overall ecosystem functioning (Walker 1992) has been established. Downed wood provides microhabitat for invertebrates (Buddle 2001, Koenings et al. 2002), small mammals (Carey and Johnson 1995, Butts and McComb 2000), and amphibians (Aubry et al. 1988, Butts and McComb 2000). In western Pacific Northwest forests, several amphibian species are strongly associated with downed wood (e.g., Dupuis et al. 1995, Butts and McComb 2000, Martin and McComb 2003). Specifically, moderate to well-decayed downed wood is an important habitat component for plethodontid salamanders, such as western red-backed salamanders (*Plethodon vehiculum*; Aubry et al. 1988, Corn and Bury 1991), clouded salamanders (*Aneides ferreus*; Bury and Corn 1988, Corn and Bury 1991) and ensatina (*Ensatina eschscholtzii*; Aubry et al. 1988, Corn and Bury 1991, Butts and McComb 2000). Temperature regimes are especially critical for these lungless salamanders because gas

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exchange and water balance occurs through the permeable surface of their skin (Feder 1983), making them highly susceptible to dehydration (Tracy 1976).

Field studies have indicated that selected temperatures for western red-backed and Dunn's salamanders (*Plethodon dunni*) average 10.4 °C (Dumas 1956). Thermal tolerances also have been documented for several plethodontid salamanders found in the Oregon Coast Range (e.g., western red-backed salamander, Dunn's salamander, clouded salamander and *Ensatina*), generally concluding that critical thermal maxima for these species are approximately 30-31 °C (Brattstrom 1963). Critical thermal maximum is a measurement of a species' thermal tolerance at which point an animal's locomotory activity becomes disorganized, becoming unable to escape from conditions that, if continued, would quickly lead to death (Spotila 1972). As temperature and moisture limits are reached in the air and ground surface, these salamanders usually retreat to subsurface refugia (Brattstrom 1963).

Recently, downed wood habitat suitability as refugia for these species has become an emerging management concern as downed wood is less available and of smaller size in managed forests (Aubry et al. 1988, Spies and Cline 1988, Rose et al. 2001). Cool, moist micro-environments provided within logs are an important habitat component for terrestrial salamanders (Bury and Corn 1988, Corn and Bury 1991, deMaynadier and Hunter 1998), providing relief from heat stress during warmer summer months, as well as nesting and foraging sites (Maser and Trappe 1984, Aubry et al. 1988, Bury et al. 1991). However, reduced canopy cover after timber harvest may result in increased temperatures within downed wood (Marra and Edmonds 1996), making it potentially unsuitable habitat for terrestrial amphibians.

Herein, we address temperature comparisons among downed wood, soil, and air environments within managed forests of western Oregon. Our primary objective was to assess an important aspect of plethodontid salamander habitat: how thermal environments within logs compare with soil and air temperatures. With large-diameter downed wood (hereafter 'large logs') recruitment declining on managed landscapes, our study was designed to determine whether smaller-diameter downed wood ('small logs') can provide similar thermal regimes to large logs. In addition, to address how lateral

distance from streams affects microclimates in downed wood and soil, we examined temperatures in small logs, large logs and soil near streams and upslope. We also measured the temperature of the air immediately surrounding each of these. Our predictions followed logical patterns of expected temperature gradients: 1) logs, being surrounded by air, would maintain warmer thermal environments relative to soil, therefore differing in their abilities to buffer against air temperature extremes; and 2) near-stream air and substrate temperature regimes would maintain cooler overall conditions relative to upslope conditions due to the moderating influence of the stream (e.g., "stream effect;" Olson et al. 2007).

Furthermore, to gain initial insights into effects of thinning and riparian buffers with varying widths, we investigated the relationships described above along three streams with differing forest management histories: 1) a narrow riparian buffer with upslope thinning; 2) a wider riparian buffer with upslope thinning; and 3) an unthinned stand.

## Study Area

Our study was conducted at an experimental forest stand in the Oregon Coast Range about 56 km northwest of Eugene, Oregon (Ten High study site: U.S. Bureau of Land Management (BLM), Eugene District; Lane Co., Benton Co.; 44°16' 50" N, 123° 31' 06" W, elevation 384-870 m). This site is part of the BLM Density Management and Riparian Buffer Study (Cissel et al. 2006) and is within the western hemlock (*Tsuga heterophylla*) vegetation zone (Franklin and Dyrness 1988). Thinning at our study site occurred in 1999. Douglas-fir (*Pseudotsuga menziesii*) dominated the stand that was naturally regenerated from clearcut harvest in 1946 and pre-commercially thinned in 1972. Other less frequent conifer species included western hemlock and western redcedar (*Thuja plicata*). Hardwoods included red alder (*Alnus rubra*) and bigleaf maple (*Acer macrophyllum*). Common understory species included sword fern (*Polystichum munitum*), Oregon grape (*Mahonia nervosa*), salal (*Gaultheria shallon*), Oregon oxalis (*Oxalis oregana*) and vine maple (*Acer circinatum*).

## Methods

Characterization of microclimate regimes at different positions relative to stream edges were attained

through continuous sampling of downed wood, soil and air temperatures along three headwater streams with different management histories: 1) one with a narrow riparian buffer (~6 m) and moderate upslope thinning to ~200 trees per hectare (tph); 2) one with a wider riparian buffer (~15 m) and moderate upslope thinning to ~200 tph; and 3) one unthinned stand (615 tph). Mean canopy cover in thinned upslopes was 67% and 98% in riparian buffers and the unthinned stand. The stream with the 6 m buffer was intermittent and 0.4 m wide (stream aspect: 260°), whereas the streams in the 15 m buffer and unthinned stand were 1.5 m wide with perennial flow (stream aspect: 176° and 99°, respectively). These three sites were selected for their homogeneous vegetation and were matched for many environmental parameters. However, we were unable to control for stream aspect, which would have direct bearing on temperatures. Additionally, we did not have treatment replication; therefore, each treatment was approached as a separate case study.

Downed wood surveys were performed along each stream cataloguing species, length, diameter, decay class and distance from stream. Following the survey, the area along each stream was divided into three spatial units. Terrestrial amphibians associated with downed wood are most-often found in moderately decayed conifer logs (e.g., Douglas-fir; Aubry et al. 1988, Corn and Bury

1991, Butts and McComb 2000). Hence only Douglas-fir logs fully resting on the forest floor and ranging between decay classes 3 and 4 (Sollins 1982) were chosen for our study. Downed wood pieces (i.e., logs) were randomly selected from the pool of conifer logs within each of these spatial units that fit the following criteria: logs with bark beginning to slough off and decaying sapwood (decay class 3) and logs with a loss of most bark and decaying heartwood (decay class 4).

During the winter of 2005, 54 dual-temperature data loggers (GPSE 301 203, A.R. Harris, Ltd., Christchurch, New Zealand) were deployed for continuous monitoring over a ten-month period, recording data hourly from December 2005 to October 2006. Eighteen data loggers were deployed along each of the three streams, with nine placed streamside (0-5 m from the stream edge) and nine placed upslope (35-40 m from the stream edge; Figure 1). Each nine-logger subset was further allocated to three small logs (0.30 to 0.45 m diameter); this range is representative of on-site trees available for potential downed wood recruitment), three large logs (0.70 to 1.00 m diameter) and three in soil. Replicates of three were used to account for environmental variation within a stand (e.g., sun exposure in thinned upslopes or canopy gaps in unthinned forest). All upslope data loggers were placed on the same side along each stream, although sides varied among

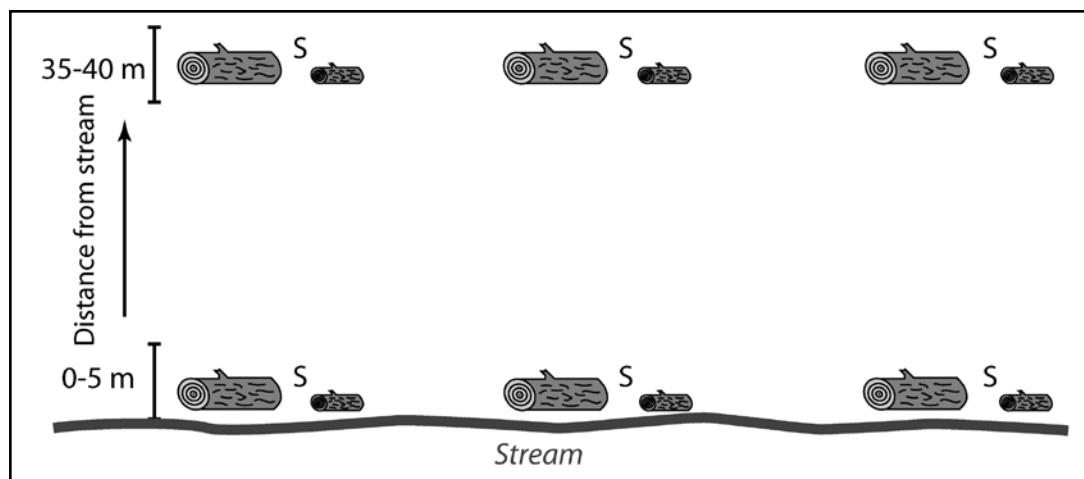


Figure 1. Data loggers were deployed along each of the three streams in a 60-year-old forest in the Oregon Coast Range. Nine data loggers were placed streamside (0-5 m from the stream bank) and nine were placed upslope (35-40 m from the stream bank). For each nine-unit subset, three were placed in large logs (0.70-1.00 m diameter), three in small logs (0.30-0.45 m diameter) and three in soil (s) locations near downed wood. Each data logger also monitored ambient air temperatures.

streams depending on where downed wood was available. Streamside data loggers were allowed to be placed on either side of the stream based on downed wood availability. Each data logger was capable of monitoring ambient air temperature, allowing for substrate-air comparisons.

To install data logger temperature sensors into downed wood, a drill was used to bore to the center of each log. Our reasoning to bore to the center of the logs was multifaceted: 1) our limited number of data loggers did not allow us to monitor multiple depths within logs; 2) as temperatures rise, terrestrial amphibians seek out cooler, moist refugia, often traveling deeper into logs (Blaustein et al. 1995) using channels in decaying wood (Jones et al. 2005); and 3) to keep position uniform among logs of different sizes. Once sensors were inserted into a log, each drilled hole was sealed at the surface to keep sensors in place. Soil temperatures were measured at a subsurface depth of 0.15 m, and air temperatures were measured 0.25 m above substrates. Air temperature sensors were protected from rain, dew and direct sunlight by an inverted opaque plastic cup mounted on a fiberglass rod.

We examined mean daily maximum temperatures of substrates and air during the month of July, which experienced the warmest temperatures over the ten-month sampling period, to investigate: 1) how small logs, large logs and soil differ in their buffering capabilities against thermal extremes that may be limiting to terrestrial salamanders; and 2) how air temperatures and thermal environments within substrates differed with distance from stream. Hourly temperature data were used to calculate daily maximum temperatures for substrates (small and large logs, soil) and air. These daily values were averaged over the month to determine mean daily maximum temperatures ( $T_{\max}$ ;  $n = 31$ ).

Mean daily maximum temperature data was analyzed using analysis of variance (ANOVA) modeled as a randomized split-split-plot design. In this design, distance from stream was considered the whole plot factor (two levels: streamside and upslope), whereas substrate type formed the first split-plot factor (three levels: small logs, large logs and soil) and temperature location as the second split-plot factor (two levels: ambient air and inside substrate). This design allowed us to test whether the differential in mean maximum temperature

between ambient air vs. internal substrate differed with substrate, distance or both (distance x substrate type x temperature location interactions). Variation among ambient air temperatures was found to be much higher than within substrates, so variance in this model was allowed to differ with location. Data were  $\log_e$  transformed to meet assumptions of normality and constant variance. Back-transformations to the original scale were performed for data presentation. All pairwise comparisons were adjusted for significance using the Tukey-Kramer procedure. The significance level for all analyses was  $P \leq 0.05$ . All statistical analyses were done using SAS v. 9.1 statistical software (SAS Institute 2004).

To examine how microclimates of these different substrates were influenced by daily air temperature fluctuations, we compared the basic statistics of mean daily differences (maximum – minimum; Chen et al. 1993). Daily maximum and minimum temperatures for air and substrate temperatures, both streamside and upslope, were calculated from hourly temperature data. Minimum temperatures were then subtracted from maximum temperatures to calculate daily differences. Daily differences were averaged for the sampling period (July,  $n = 31$ ) resulting in mean daily differences ( $T_{\Delta}$ ).

Finally, to gain additional insight to how these different substrates reacted against temperature extremes, temperature regimes of small and large logs, soil and ambient air temperatures were plotted and visually inspected for patterns of temperature change.

## Results

### Six-Meter Buffer Stream

Although there was no three-way interaction of distance x substrate type x temperature location (Table 1), a substrate type x temperature location interaction indicated that the differential in mean daily maximum temperatures ( $T_{\max}$ ) between ambient air and internal substrate varied among substrates (Table 1). A main effect of distance (Table 1) indicated overall  $T_{\max}$  varied with distance from stream. Upslope  $T_{\max}$  was estimated to be 17-24% higher than those streamside. Streamside and upslope temperature differentials (air  $T_{\max}$  / substrate  $T_{\max}$ ) for soils were 16-29% greater than those of large logs ( $t_{12} = 3.13$ ,  $P = 0.008$ ) indicating that soils buffered against thermal extremes

TABLE 1. Main effects and interactions from split-split-plot analysis of variance (ANOVA) for mean daily maximum temperatures of air, large logs, small logs, and soil temperatures over the warmest month of 2006 (July) along three headwater streams with different management histories in western Oregon: 1) one with a 6-m buffer and upslope thinning; 2) one with a 15-m buffer and upslope thinning; and 3) one in an unthinned stand. ST = substrate type (small log, large log or soil), D = distance from stream (streamside or upslope), TL = temperature location (ambient air or internal substrate).

Treatment	Source	F	ndf	ddf	P
6-m buffer	ST	2.65	2	12	0.1
	D	41.25	1	12	<0.0001
	TL	549.98	1	12	<0.0001
	ST x D	2.82	2	12	0.1
	ST x TL	5.05	2	12	0.02
	D x TL	4.19	1	12	0.06
	D x ST x TL	0.29	1	12	0.7
15-m buffer	ST	0.91	2	12	0.4
	D	45.24	1	12	<0.0001
	TL	525.5	1	12	<0.0001
	ST x D	1.06	2	12	0.4
	ST x TL	1.94	2	12	0.2
	D x TL	16.56	1	12	0.002
	D x ST x TL	0.18	2	12	0.8
Unthinned	ST	17.16	2	12	0.0001
	D	30.98	1	12	0.0001
	TL	884.22	1	12	<0.0001
	ST x D	0.62	2	12	0.5
	ST x TL	14.93	2	12	0.0006
	D x TL	0.09	1	12	0.8
	D x ST x TL	1.24	2	12	0.3

better than large logs. However, no significant differences were seen between differentials of small and large logs ( $t_{12} = 1.11, P = 0.3$ ), or soil and small logs ( $t_{12} = 2.02, P = 0.07$ ).

When comparing mean daily temperature differences (maximum – minimum;  $T_{\Delta}$ ) of air and substrate temperatures,  $T_{\Delta}$  appeared to be greater in the upslope along the 6-m buffer stream (Table 2; Figure 2: A.1 and A.2). Although differences were small, streamside and upslope small logs tended to experience greater  $T_{\Delta}$  when compared to large logs and soil (Table 2), whereas soil had a tendency to experience slightly greater  $T_{\Delta}$  when compared to large log  $T_{\Delta}$ . Daily temperature fluctuations were seen with small log and soil temperature profiles, whereas profiles of large logs were more stable and experienced little to no

fluctuation (Figure 2: A.1 and A.2). As predicted, temperature profiles of small logs experienced greater variation compared to soils, especially upslope outside the buffer (Figure 2: A.1 and A.2). Large logs took longer to reach maximum temperatures and longer to cool off, exhibiting a lag time of about two days behind small logs (Figure 2: A.1 and A.2).

### Fifteen-Meter Buffer Stream

Similar to the 6-m buffer stream, there was no three-way interaction of distance x substrate type x temperature location seen along the 15-m buffer stream (Table 1). However, a distance x temperature location interaction indicated that the differential in  $T_{\max}$  between ambient air and internal substrate varied with distance from stream (Table 1). Upslope substrate  $T_{\max}$  was estimated to be 2-20% higher than streamside and upslope air  $T_{\max}$  was 15-31% higher than streamside. No significant temperature differentials were observed between small logs and large logs ( $t_{12} = 0.52, P = 0.6$ ), small logs and soil ( $t_{12} = 1.38, P = 0.2$ ) or large logs and soil ( $t_{12} = 1.91, P = 0.08$ ).

When comparing  $T_{\Delta}$  of air and substrates along the 15-m buffer stream, differences upslope had a tendency to be greater compared to streamside (Table 2). Large logs maintained a smooth temperature profile relative to small logs and soil, both streamside and upslope (Figure 2: B.1 and B.2). Large logs also experienced a lag time in heating and cooling relative to small logs, similar to what was seen along the stream with the 6-m buffer (Figure 2). Mean daily temperature differences among streamside substrates were similar; however, upslope large logs tended to experience the least  $T_{\Delta}$  relative to the other substrates (Table 2).

### Unthinned Stand

As with the other two streams, we did not see a distance x substrate type x temperature location interaction in the unthinned stand (Table 1). However, similar to the 6-m buffer stream, a substrate type x temperature location interaction indicated that the differential in  $T_{\max}$  between ambient air and internal substrate varied among substrates (Table 1). Also, a main effect of distance (Table 1) indicated overall  $T_{\max}$  varied with distance from stream. These differences were subtle in the unthinned stand where upslope  $T_{\max}$  was estimated

TABLE 2. Means (SE) of daily maximum ( $T_{\max}$ ), minimum ( $T_{\min}$ ) and differences (maximum – minimum,  $T_{\Delta}$ ) for streamside and upslope air, large logs, small logs, and soil temperatures ( $^{\circ}\text{C}$ ) along three headwater streams with different management histories in western Oregon: 1) one with a 6-m buffer and upslope thinning; 2) one with a 15-m buffer and upslope thinning; and 3) one in an unthinned stand over the warmest month of 2006 (July;  $n=31$ ).

Treatment	Location	Variable	$T_{\max}$	$T_{\min}$	$T_{\Delta}$
6-m buffer	Streamside	Air	26.06 (2.50)	13.79 (0.22)	12.27 (2.66)
		Large log	17.48 (0.53)	17.03 (0.58)	0.45 (0.07)
		Small log	18.16 (0.49)	16.92 (0.37)	1.24 (0.33)
	Upslope	Soil	15.86 (1.00)	15.13 (0.22)	0.73 (0.48)
		Air	33.25 (3.00)	13.06 (0.40)	20.19 (2.73)
		Large log	22.42 (1.38)	21.67 (1.14)	0.75 (0.24)
		Small log	20.30 (2.03)	18.30 (2.27)	2.00 (0.29)
		Soil	18.16 (1.09)	16.80 (0.54)	1.36 (0.59)
		Air	22.96 (0.80)	13.65 (0.18)	9.30 (0.77)
15-m buffer	Streamside	Large log	16.93 (0.90)	16.08 (0.96)	0.85 (0.46)
		Small log	16.24 (0.33)	15.38 (0.39)	0.86 (0.06)
		Soil	15.71 (0.80)	14.86 (0.32)	0.85 (0.23)
	Upslope	Air	30.08 (3.24)	13.43 (0.18)	16.65 (3.20)
		Large log	18.50 (0.80)	17.80 (0.85)	0.70 (0.23)
		Small log	19.34 (0.36)	17.49 (0.57)	1.86 (0.29)
		Soil	17.19 (1.31)	15.63 (0.47)	1.56 (0.90)
		Air	21.77 (0.83)	12.66 (0.16)	9.11 (0.73)
		Large log	16.16 (0.66)	15.74 (0.67)	0.41 (0.17)
Unthinned	Streamside	Small log	15.75 (0.62)	14.87 (0.35)	0.89 (0.28)
		Soil	13.54 (0.89)	13.13 (0.80)	0.41 (0.13)
		Air	23.14 (0.33)	12.98 (0.21)	10.16 (0.21)
	Upslope	Large log	16.44 (0.45)	16.00 (0.47)	0.44 (0.02)
		Small log	16.59 (0.14)	15.24 (0.58)	1.35 (0.62)
		Soil	14.84 (0.25)	14.15 (0.20)	0.69 (0.07)

to be 3-8% higher than streamside. Although there were no differences between small and large log differentials ( $t_{12} = 0.33$ ,  $P = 0.7$ ), it was estimated that streamside and upslope differentials for soil were 16-24% greater than those of small logs ( $t_{12} = 4.89$ ,  $P = 0.0004$ ) and 15-23% greater than those of large logs ( $t_{12} = 4.56$ ,  $P = 0.0007$ ) indicating that soil buffered against thermal extremes more efficiently than either small or large logs in the unthinned stand.

Mean daily differences in air and substrate temperature between streamside and upslope transects were slight along the stream in the unthinned stand (Table 2; Figure 2: C.1 and C.2). Much less temperature variation was experienced along this stream compared to along the 6-m and 15-m buffer streams (Table 2; Figures 2). Very little daily variation was seen in temperature profiles of large logs, whereas small logs tracked daily changes in air temperature quite closely and soils did so more subtly (Figure 2: C.1 and C.2). Although  $T_{\Delta}$  among substrates was minimal, small logs tended to experience the greatest  $T_{\Delta}$ , whereas  $T_{\Delta}$  for large logs and soil were similar (Table 2).

## Discussion

Our study is one of the first to address microhabitat temperature profiles in managed forests of the Pacific Northwest. Our results support previous studies that reported distance from stream had an influence on temperature patterns, as microclimate gradients extended from the stream to upslope, with cooler conditions along streams (Anderson et al. 2007). Although we cannot make statistical comparisons among conditions along our three streams due to a lack of treatment replication, it should be noted that there was a pattern of cooler streamside conditions gradually extending into upslope areas, increasing as buffer widths widened. This is illustrated along the stream in the unthinned stand where streamside and upslope temperature differences were slight relative to conditions along the stream with the 6-m buffer. Interestingly, there was an interaction of distance and temperature location (ambient air vs. internal substrate) for  $T_{\max}$  along the stream with the 15-m buffer. However, the ratio of ambient air to substrate temperature was not detectably different streamside versus upslope along either the

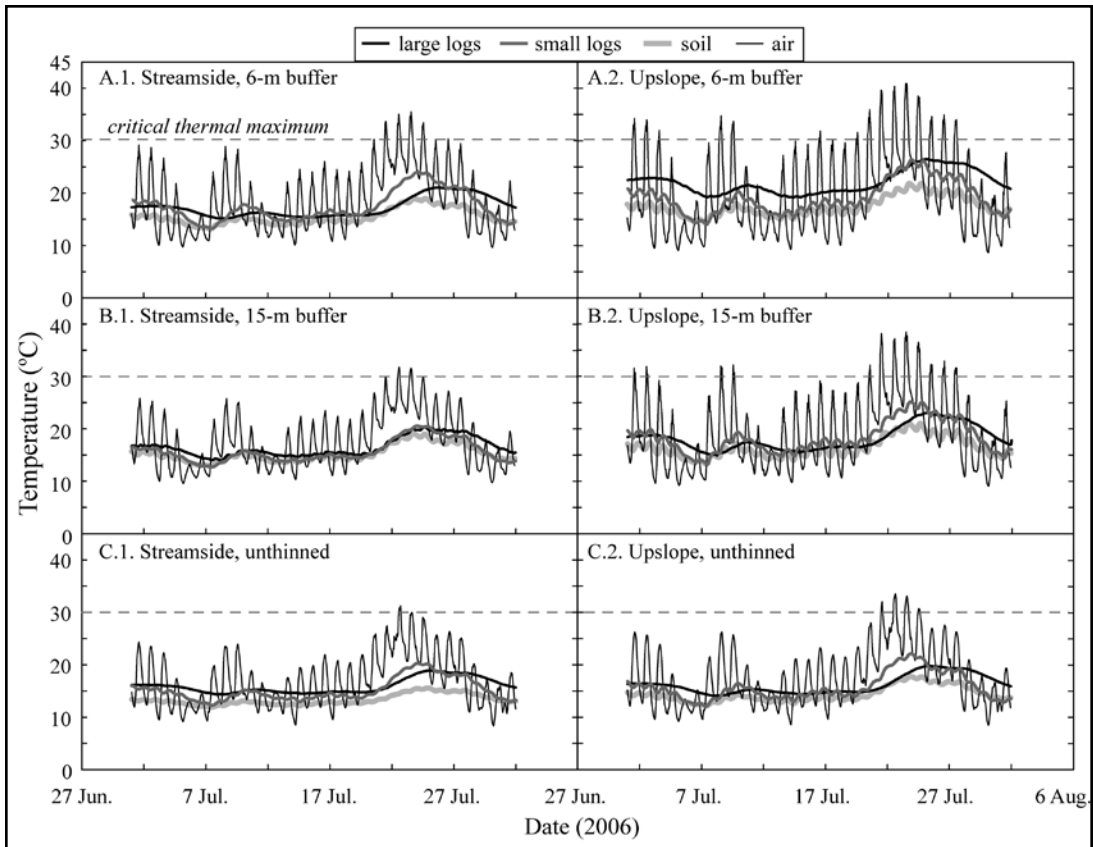


Figure 2. Streamside (0-5 m) and upslope (35-40 m) temperature profiles of small- and large-diameter logs, soil and air during July along three headwater streams with different management histories in western Oregon: A) one with a 6-m buffer and upland thinning (1. streamside, 2. upslope); B) one with a 15-m buffer and upland thinning (1. streamside, 2. upslope); and C) one in an unthinned stand (1. streamside, 2. upslope). Average critical thermal maximum for western plethodontid salamanders ( $\sim 30^{\circ}\text{C}$ ; Brattstrom [1963]) is shown by a dotted line.

stream with the 6-m buffer or in the unthinned stand. This may have been due to differences in stream aspect.

Although previous research on thermal regimes of downed wood is limited, logs in an old-growth stand in northwestern Washington were shown to protect from thermal extremes and water loss. Both large and small moderately decayed logs (decay class 3) responded similarly, maintaining cooler internal temperatures compared to surface temperatures (Marra and Edmonds 1994). In our three case studies, all substrates (small logs, large logs and soil), both streamside and upslope, protected against thermal extremes reached by air temperatures. During the warmest month of our sampling period (July, 2006), mean daily maximum temperatures ( $T_{\text{max}}$ ) for substrates along all three

streams were lower compared to air  $T_{\text{max}}$  (Table 2). This further illustrates the important role these substrates play in providing refugia for animals, such as plethodontid salamanders, from extreme temperatures in managed forests.

When contrasting ambient air  $T_{\text{max}}$  against substrate  $T_{\text{max}}$ , we saw varying results along each of the three streams. Along the stream with the 15-m buffer we saw no significant differences among buffering capabilities of substrates against thermal extremes. Conversely, along both the stream with the 6-m buffer and in the unthinned stand, soil appeared to be the more efficient buffer among substrates. However, daily temperature fluctuations were evident in small logs and in soil temperature profiles, whereas these fluctuations were either not present or in lower frequency and amplitude in

large logs. Additionally, all streamside substrates as well as large logs in the upslope exhibited more constant temperature profiles and less overall daily variation. These temperature profiles are likely to have biological relevance for fauna reliant on these forest substrates. However, the effects of temperature variation on terrestrial amphibians and their prey warrants further study.

Patterns seen during our study follow expectations because direct solar radiation is a major source of air and soil heating (Anderson et al. 2007). The amount of solar radiation reaching the forest floor is primarily dependent on overstory canopy cover, height and species composition (Brosofske et al. 1997). In all three of our case studies, air and substrate temperatures were consistently cooler in areas where canopy cover was retained (e.g., riparian buffers and unthinned upslope).

As would be expected, air  $T_{\max}$  was higher than substrate  $T_{\max}$ . In all three case studies, maximum air temperatures above logs and soils during July exceeded critical thermal maxima (CTM) for western plethodontid salamanders. This was especially seen in the thinned upslopes. Conversely, log and soil temperatures failed to reach CTM under all conditions, demonstrating the ability of soil, small logs and large logs to protect against thermal extremes that are harmful to plethodontid salamanders. Our findings support Blessing et al. (1999), who monitored one 0.5 m diameter log that held a clutch of Van Dyke's salamander (*Plethodon vandykei*) eggs and concluded that internal log temperatures were cooler and more constant than ambient air temperatures and that the log protected the eggs against thermal extremes.

Although removal of overstory reduces moisture retention and increases internal temperatures of downed wood (Marra and Edmonds 1996), recruitment of smaller-diameter downed wood (> 0.3 m) and partial canopy retention (e.g., moderate thinning) may be a viable plethodontid salamander habitat management alternative as larger logs disappear from managed landscapes over time. Further considerations relative to small logs are: 1) their faster decay rates (Stone et al. 1998); and 2) they may desiccate at a faster rate relative to large logs, depending on their stage of decay (Triska and Cromack 1980, Marra and Edmonds 1996). Hence, increased downed wood recruit-

ment frequencies of smaller logs and increased canopy retention may be needed to provide stable quantities of decaying log habitats on the forest floor for these taxa.

Canopy removal also may result in increased soil temperatures (e.g., clearcut; Marra and Edmonds 1996, Chen et al. 1993). Our study demonstrated that at 0.15 m below the surface, soils in thinned stands may provide refugia from temperature extremes. Although this may vary depending on structure and composition of stands prior to harvest, and timber harvest prescriptions (Aubry 2000), this finding may explain the apparent broad microhabitat associations of some plethodontid salamanders that are found within a variety of substrate types (e.g., western red-backed salamander [Ovaska and Gregory 1989, Aubry 2000], ensatina [Aubry 2000, Rundio and Olson 2007]). However, other species are more habitat specific, such as the clouded salamander, which appears to be largely associated with downed wood (Bury and Corn 1988, Corn and Bury 1991).

Although cool, moist microhabitats are often available deep in burrows, logs and rock crevices, the availability of any one of these microhabitats alone may be insufficient to support viable plethodontid salamander populations. As moisture decreases, these salamanders likely become limited in their activities. Exposed microhabitats (e.g., leaf litter, soil surface, rock faces, vegetation) are where most foraging and probably courtship occurs (Feder 1983). If surface conditions are dry, salamanders remain beneath cover objects (Cunningham 1960, Jaeger 1980), choosing progressively larger cover objects (e.g., downed wood) until conditions become too dry, finally retreating underground (Cunningham 1960, Taub 1961, Heatwole 1962), where little feeding occurs (Feder 1983). Therefore, it is essential to maintain a variety of habitats within managed forests (Aubry 2000).

Further research is needed to gain a better understanding of the importance of temperature stability for plethodontid salamanders, and how reduced canopy cover affects temperature regimes of small logs, large logs and soils as suitable plethodontid salamander habitat relative to other ecological functions (e.g., prey availability, moisture regimes).



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